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MORPHOFUNCTIONAL CHANGES OF OVARIOLES OF THE BLOOD-SUCKING MOSQUITO
(DIPTERA, CULICIDAE) DURING OOGENESIS. 2. ABORTIVE OOGENESIS

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MORPHOFUNCTIONAL CHANGES OF OVARIOLES OF THE BLOOD-SUCKING MOSQUITO
(DIPTERA, CULICIDAE) DURING OOGENESIS. 2. ABORTIVE OOGENESIS

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→ In a previous report [6] we examined the normal oogenesis of blood-sucking mosquitos using the example of 15 species, as well as the methods of its supravital study. This work presents data on abortive oogenesis in these same species, obtained with the application of analogous methodologies. /55

Abortive oogenesis is a process of degeneration of the follicles in individual ovarioles, and occurs parallel with normal oogenesis in other ovarioles of the ovary. At the even ovariole cycle, as a result of degeneration, so-called extasias are formed instead of the ovum. Depending on the character and time of feeding of the female, we may distinguish 3 variants of degeneration: Pregonotrophic, agonotrophic, and gonotrophic, and progonotrophic [7], agonotrophic [5] and gonotrophic [5] extasia. Moreover, extasia may be present in the ovarioles which we have called vestigial [8] and aberrant [9]. The former represent any of the indicated forms of extasia pushed under the ovariole membrane by the emerging egg. Aberrant extasia are formed with an anomalous condition of the ovarioles. *Fig. 1, 2, 3, 4, 5*

Pregonotrophic degeneration. In studying *Aedes dorsalis* Meig in the northern population, we found degeneration of the follicles from N and I stage of development according to Christofers-Mer. The degenerating follicles appear immediately after emergence of the female from the chrysalis, and prior to her taking any food. The follicle turns into a small compact formation with luteal inclusions, brightly colored from neutral red to crimson color, and called pregonotrophic extasia (Fig. 1, a,b, cf. on insert) [7]. The ovariole may remain in this form until the end of the female's life (Fig. 1,c). In *Anopheles messeae* Fall. the form of pregonotrophic extasia differs from that of *Ae. dorsalis*. The extasia are oval, located to the side of the central axis of the ovariole, and its terminal processes are longer (Fig. 2, cf. on insert). Pregonotrophic extasia in 1-5 ovarioles of the ovary were found in 97% of the studied



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Ae. dorsalis, in 1-2 ovarioles--in 93% of *Ae. punctor* Kirby and *Ae. communis* de Geer, and in 90% of *An. messeae*.

The literature contains descriptions of ovariole extasia which, judging by everything, are pregonotrophic in our sense [3, 4, 19]. Evidently, the phenomenon of pregonotrophic degeneration is typical for female blood-sucking mosquitos. Evidently, pregonotrophic degeneration of the follicles immediately after the female's emergence from the chrysalis may occur in connection with the elimination of presumptive egg chambers with genetic or some other defects. It is specifically this which serves as one of the explanations for atresia of follicles in mammals [17]. /56

Agonotrophic degeneration. Agonotrophic degeneration of follicles was first observed in laboratory cultures of mosquitos [5, 20, 22, 25]. Such degeneration was described non-gonoactive hibernating females [3, 4]. In a number of works there are descriptions of degenerating follicles and extasia which today may be evaluated as agonotrophic [1, 2, 14, 24]. We observed agonotrophic degeneration in females of laboratory cultures as well as in nature. The females of the northern population of *Ae. dorsalis* in nature often do not have the opportunity to fly out in search of nourishment and to drink blood for a long time from the moment of imago hatching. This is determined by the weather. In such females, along with the ovarioles, whose follicles developed normally or had pregonotrophic extasia, there were ovarioles whose follicles degenerated with formation of agonotrophic extasia [7]. One of the main indicators of agonotrophic degeneration, morphologically most reliable in *Ae. dorsalis*, *Ae. communis* and *Ae. punctor*, may be considered the retention of the terminal process in an unchanged state, which was also noted for the laboratory *Culex pipiens pipiens* L. [10]. In female *An. messeae* in nature, agonotrophic degeneration was not found. However, in females hatched from chrysalis collected in nature and kept in the laboratory on a carbohydrate diet, by the 7-10th day the first ovarioles with agonotrophically degenerating follicles were manifested. In females taken from nature who had previously laid eggs and who had been transferred to the laboratory, on the 5th day there were also 1-2 ovarioles with degenerating follicles (fig. 3). Unlike the ovarioles with pregonotrophic degeneration, in the ovarioles with agonotrophically degenerating follicles the next follicle separates from the germarium and continues to develop normally.



Fig. 3. Agonotrophic degeneration of the follicle in *Anopheles messeae*. 1 - germarium; 2 - follicle of the III order; 3 - degenerating follicle of the II order; 4 - egg sac; 5 - trachea. x 40, gomai 3.

The appearance of agonotrophic extasia may represent a typical reaction of females to deterioration of external conditions. Evidently, agonotrophic degeneration in nature must be manifested more often in female mosquitos not bound by their place of habitation with collection of food-animals. The most widely used explanation of oosorption consists of the following. When there are insufficient nutrient substances in periods of prolonged carbohydrate feeding of females or with a small amount of sucked blood, certain oocytes are subjected to resorption, which provides additional material for the development of other oocytes [3, 11]. We know that the rate of synthesis of triglycerides is similar in female mosquitos regardless or whether they have fed on carbohydrates or proteins. Blood nourishment of mosquitos has no advantages over carbohydrate from the standpoint of the fat metabolism [16]. Therefore, this explanation is not unfounded. Moreover, as in the case with pregonotrophic degeneration, the elimination of individual oocytes is possible if their defects are manifested in later periods of their development. Follicles

with such oocytes may be subject to resorption also if the remale takes a full portion of blood. With sufficiently prolonged carbohydrate feeding of the females, general degeneration of most of the ovarioles in the ovaries is observed. Therefore, agonotrophic degeneration may be the result of age changes in the mechanisms of hormonal regulation of oogenesis, which is what causes general degeneration of the ovarioles in the ovary at the end of the female's life. Thus, agonotrophic extasia in its nature is nonuniform and formed for different reasons in periods of prolonged carbohydrate feeding.

Gonotrophic degeneration. In female mosquitos of the studied species we found typical pictures of gonotrophic degeneration of follicles, described in the literature [5, 14, 23]. With supravital staining of the preparations with neutral red, 1-2 small inclusions are stained in the epithelial cells of normally developing follicles. These are uniformly distributed over the surface of the follicle. At the initial stages of degeneration of the follicles the order of distribution of the stained inclusions is disrupted. The follicles may degenerate from the II-III stages. The cells of the follicular epithelium become enlarged, luteals of various size appear in them, which are heavily stained with neutral red. Then the epithelium is subjected to autolysis, intima collects in the folds, and gonotrophic extasia remains at the place of the follicle (Fig. 4, cf. on insert). In most cases the terminal processes change as in normal oogenesis, losing their cell structure. Parallel with the degeneration of the follicle of the I order, the follicle of the II order separates from the germarium. By the beginning of the next gonotrophic cycle the next follicles of normal ovarioles [9] in which the eggs have matured or the preceding follicles have degenerated, are at the same stage of development (Fig. 5, cf. insert). In the ovariole in which all the follicles have begun to degenerate from a single stage, the final expansion (extasia) always contains more luteal inclusions than the preceding one. If follicles from various stages of development are subjected to degeneration, extasia of various size may be seen in one ovariole. In this case the extasia at the site of follicle of the I order may be greater than the rest (Fig. 6, cf. on insert). Often follicles degenerate from different stages of development in one ovary. In some ovarioles of a normal type the follicles are subject to degeneration at each cycle. In 81.8% of the

female *Ae. dorsalis* at cycle I the follicles degenerate in 9.5% of the ovarioles with formation of gonotrophic expansions (extasia). In the southern population of *An. messeae* females have been found which have laid eggs 1-6 times. In the ovaries of females of each age group, ovarioles have been found with the corresponding number of gonotrophic expansions (Fig. 7). At the I cycle, 78.2% of the females had one gonotrophic extasia in 10.8% of the ovarioles. After the IV cycle, all the females had gonotrophic extasia. On the average, 18% of the normal ovarioles of ovaries had 1-4 extasia.

In the literature there are a number of interesting publications devoted to clarifying the effect of various factors on the processes of oogenesis, including on the induction of oosorption [11, 12, 14, 19, 21]. The pregono-, agono- and gonotrophic ecstasia which we have examined are strictly distinguished by time of appearance in the ovaries of the female mosquitos. The question of morphological diagnostics of the extasia of various types still remains unclear. Previously it was believed that these expansions may be the result of normal as well as abortive oogenesis. Forms which were clearly defined and distinguished from each other were ascribed to them. Extasia at the site of a released egg §"common light small expansions"¶ were distinguished from degenerative ones by the fact that they were filled with "degenerated mass" [3]. Today we may rightly consider the formation of extasia in ovarioles only as a result of degeneration of follicles in abortive oogenesis may be considered a proven fact. The amount of inclusions in the extasia depends only on the progress in time of the processes of follicle cell lysis. In practice, researchers were always dealing only with degenerative extasia. This is associated with the incorrect assumption that the eggs in principle may pass through the terminal process, as through a tube. Moreover, the undeveloped methodology of preparing ovaries with needles did not make it possible to evaluate the real portion of ovarioles with extasia in the entire ovary. It was assumed that all ovarioles must have these expansions. Since the structure of the ovarioles was often disrupted during preparation with needles, the absence of expansions was explained by the imprecise work of the researcher. Pregono- and agonotrophic extasia were most often overlooked due to their small numbers.

There is an opinion that oosorption in insects, characterized by

the cessation of vitellogenesis and the degeneration of protein-containing /58 oocytes, including their surrounding cells, is a part of the system controlling the functioning of the ovaries, and not a deviation from the norm [11]. Here it is believed that resorption of the oocytes represents a process of "preserving the untouched resources", which may be used in the future. In connection with this notion, the concept of "developmental gates" was developed [13], which was experimentally confirmed on the green flesh fly *Lucilia cuprina* Wied. [13] and the blood-sucking mosquitos [14]. Its essence consists of the fact that there are periods of delay in development of the oocytes, which do not affect subsequent maturation. In mosquitos, 5 such periods have been isolated.....

(Translator's note: Page 59, the conclusion of this article, is missing from foreign text. In addition, Figures 1, 2, 4, 5, 6 referred to as being on inserts are missing.)

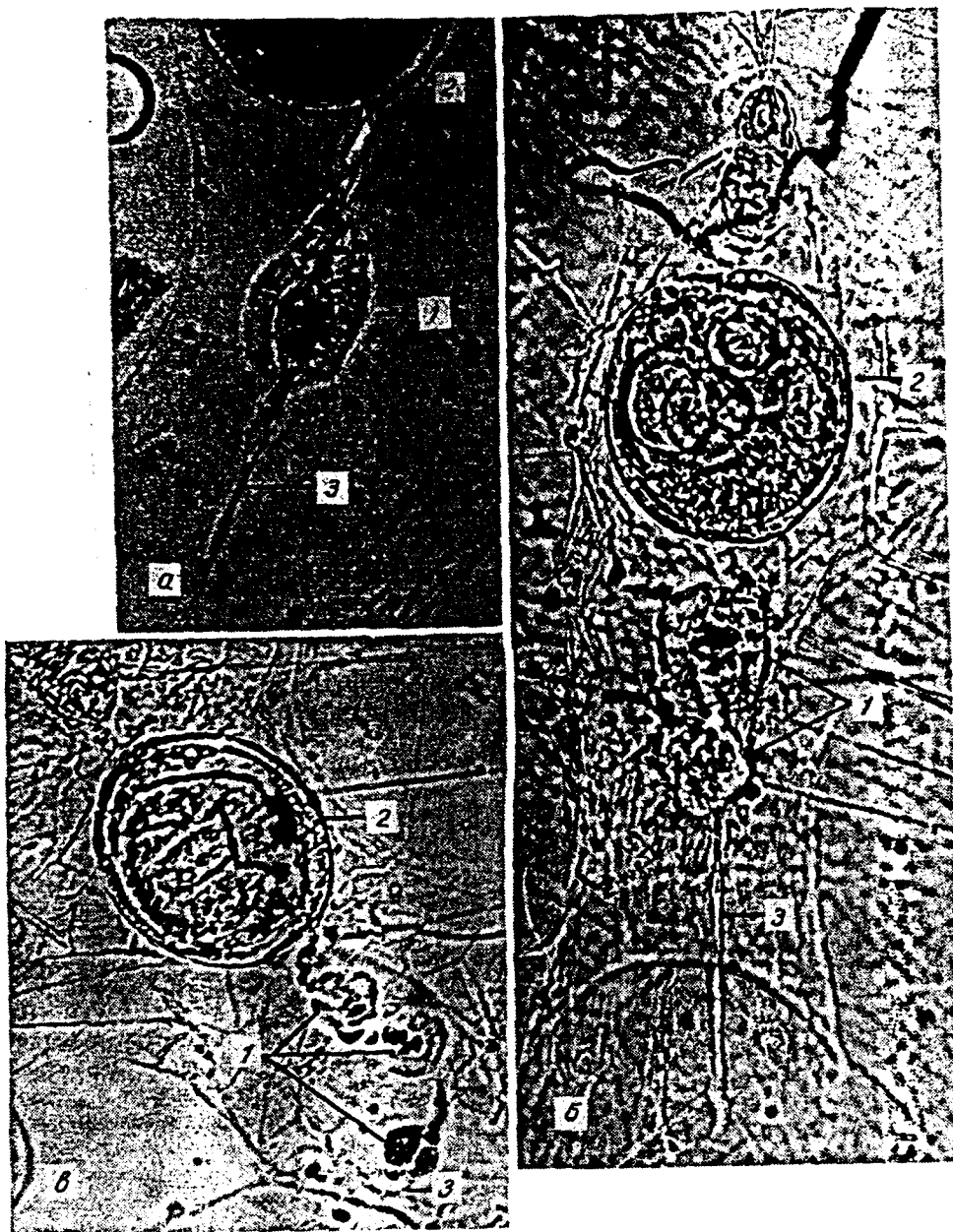


Fig. 7. Ovarioles of female *Anopheles messeae* which have performed a different number of gonotrophic cycles.

a - after 1 cycle; b - after 2 cycles; c - after 3 cycles; d - after 4 cycles [8]; e - after 6 cycles. 1 - gonotrophic extasia; 2 - follicle; 3 - terminal process. Mag. a,c, - 40, gomal 5; mag. c-e - 40, gomal 3.

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